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Aquatic Plant Control Research Program

Effects of Convective Hydraulic Circulation on Phosphorus Transport in Aquatic Macrophyte Beds

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Prepared for Headquarters, U.S. Army Corps of Engineers

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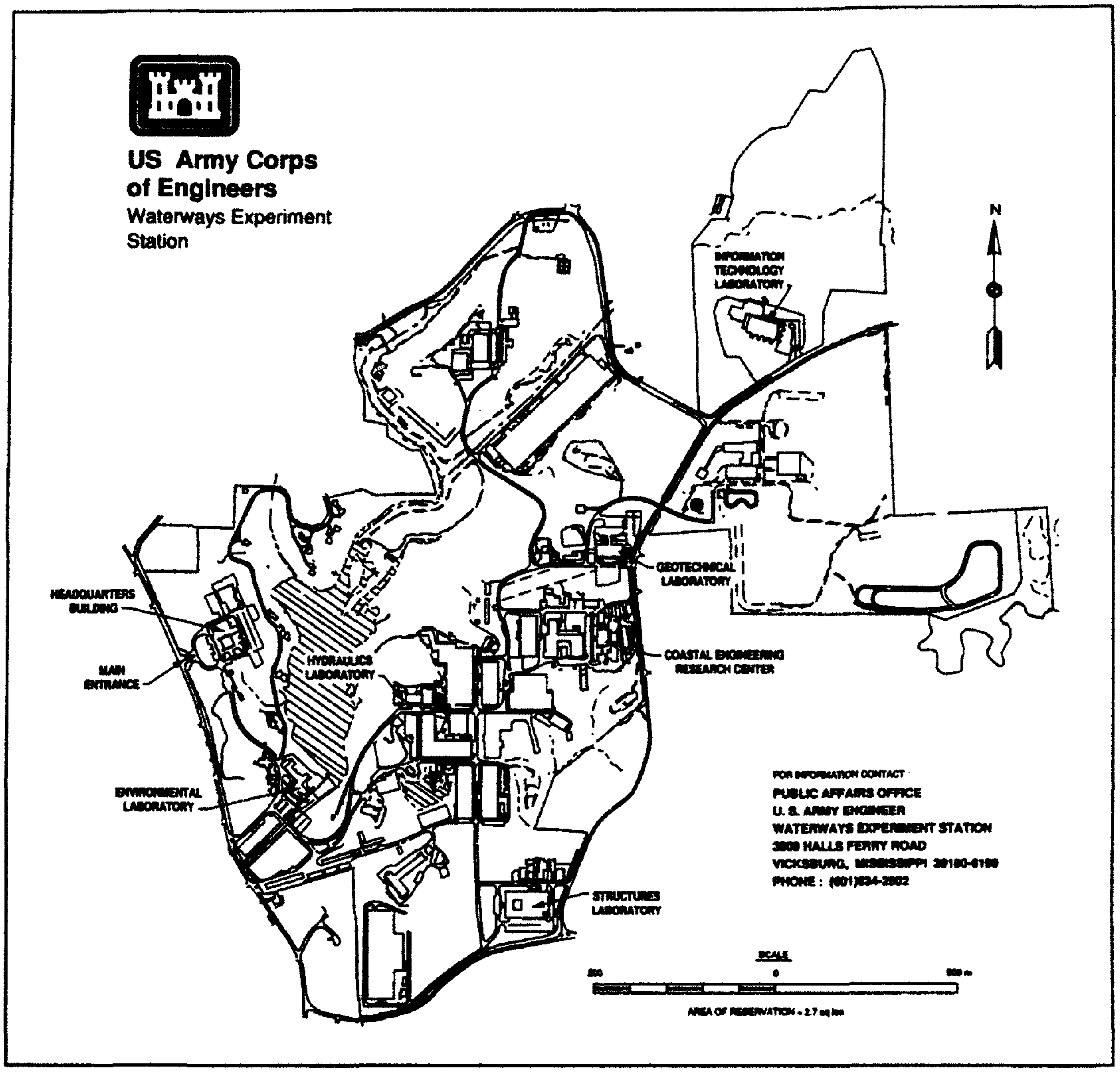

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Contents

Preface

The work reported herein was conducted as part of the Aquatic Plant Control Research Program (APCRP). The APCRP is sponsored by the Headquarters, U.S. Army Corps of Engineers (HQUSACE), and is assigned to the U.S. Army Engineer Waterways Experiment Station (WES) under the purview of the Environmental Laboratory (EL). Funding was provided under Department of the Army Appropriation No. 96X3122, Construction General. The APCRP is managed under the Environmental Resources Research and Assistance Programs (ERRAP), Mr. J. L. Decell, Manager. Mr. Robert C. Gunkel was Assistant Manager, ERRAP, for the APCRP. Technical Monitor during this study was Mr. James W. Wolcott, HQUSACE.

The study was conducted and the report prepared by Mr. William F. James and Dr. John W. Barko of the Aquatic Processes and Effects Group (APEG) of the EL. Mr. J. Carroll, Mr. J. Brown, Ms. M. Donath, Mr. H. Eakin, Ms. A. Harter, Ms. Y. Hartz, Ms. B. Nelson, Mr. R. Olewinski, Ms. H. White, and Ms. E. Zimmer provided technical assistance during the studies. Drs. R. Gaugush, G. Nürnberg, and C. Smith provided technical review of this work. This work was also reviewed anonymously by editors of the journal *Limnology and Oceanography*, in which major findings were published earlier.

The investigation was conducted under the general supervision of Dr. John Harrison, Director, EL, and Mr. Donald L. Robey, Chief, Ecosystem Research and Simulation Division, and under the direct supervision of Drs. Thomas L. Hart and Richard E. Price, Chiefs, APEG.

At the time of publication of this report, Director of WES was Dr. Robert W. Whalin. Commander was COL Leonard G. Hassell, EN.

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1 Introduction

Most investigations of internal phosphorus (P) loading in lakes have concentrated on P release from profundal sediments under anaerobic conditions (e.g. Riley and Prepas 1984, Nürnberg 1987). However, recent studies have shown that P can also be released from littoral sediments under aerobic conditions (Twinch and Peters 1984, Drake and Heaney 1987). Phosphorus released during the senescence of aquatic macrophytes constitutes another potential source of internal P loading from the littoral zone (Barko and Smart 1980, Carpenter 1980). Since internal P loading from littoral macrophyte beds may significantly influence the P economy of aquatic systems, particularly small lakes (Prentki et al. 1979), it is important to evaluate horizontal P exchanges between littoral and pelagic zones of these systems (James and Barko 1991).

We report the results of seasonal investigations of P exchange between the littoral and pelagic zones of Eau Galle Reservoir, Wisconsin, driven by nighttime convective circulation. Because of the importance of P gradients in affecting P flux rates during these periods of circulation, we examine profiles of P both in the sediment and in the overlying water column. Rates of P release from littoral sediments, affected by both pH and oxygen as a function of macrophyte metabolism, are estimated from results of laboratory incubation studies employing the use of intact sediment cores. The objective of this report is to expand earlier findings (James and Barko 1991) with greater attention to both P release from littoral sediments and climatic and limnological conditions influencing littoral-pelagic P dynamics during nighttime convective circulation.

2 Methods

Phosphorus Release from Littoral Sediments

Rates of soluble reactive P (SRP) release from littoral sediments were measured in the laboratory at pH values ranging from 8.0 to 10.0 under both aerobic and anaerobic conditions, using intact sediment cores collected from macrophyte beds within the littoral zone. Three replicate cores, each containing a sediment volume of 330 cm^3 (6.5 cm in diameter, 10 cm high), were collected in acrylic sediment core liners. The overlying water was carefully drained from each sediment core and filtered through a glass-fiber filter (Gelman A-E), with 300 ml then siphoned back onto the sediment without causing sediment resuspension.

The sediment incubation systems consisted of sediment and overlying water contained in core liners that were sealed with rubber stoppers. These incubation systems were placed in a darkened environmental chamber (Psychrotherm) and incubated at 20 °C for 1 to 2 weeks.

The oxidation-reduction environment in each system was controlled by gently bubbling either air (aerobic) or nitrogen (anaerobic) through an air stone placed just above the sediment surface. Bubbling action ensured complete mixing of the water column but did not disrupt the sediment. An automated, recording pH controller (New Brunswick) was used to maintain the pH at a constant value in each incubation system through additions of either sulfuric acid (0.1 M) or sodium hydroxide (0.1 M).

Water samples for SRP determinations were collected daily from the center of each incubation system using an acid-washed syringe and were immediately filtered through a 0.45-μm membrane syringe filter. The water volume removed from each system during sampling was replaced by addition of distilled water adjusted to the oxidation-reduction and pH conditions of the incubation system. These volumes were accurately measured to adjust SRP for dilution effects. Rates of SRP release from littoral sediments (mg m^{-2} day^{-1}) were calculated as the change in SRP in the overlying water divided by time and the area of the sediment core liner.

P Concentrations in Interstitial Water of Littoral Sediments

Three replicate sediment peepers, similar to those described in Shaw and Prepas (1989), were placed in the sediments at station 2 (Figure 1) in May, July, and August 1989 to examine seasonally the vertical patterns of P concentration in the interstitial water of littoral sediments in macrophyte beds. Acrylic sediment peepers contained six chambers spaced at 2-cm intervals.

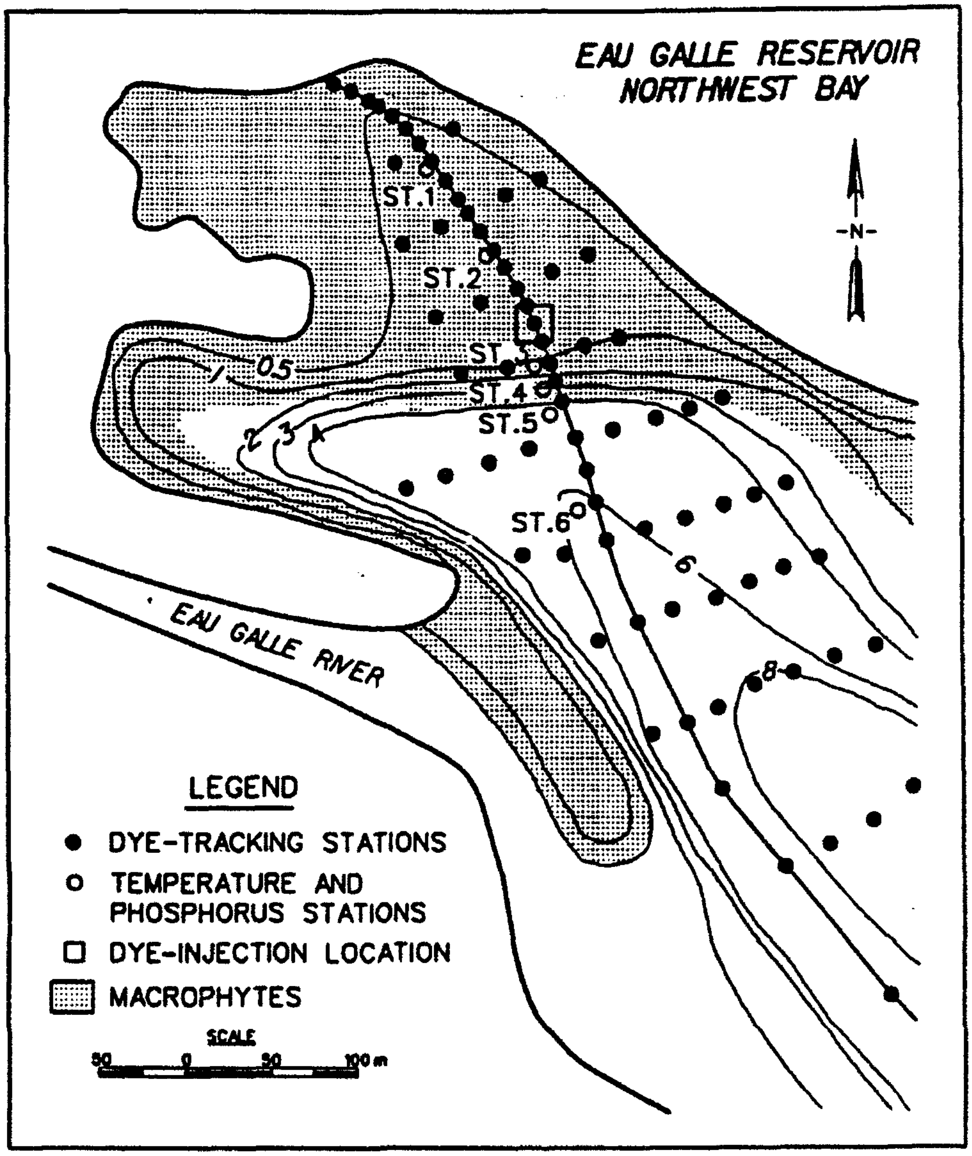

Figure 1. Morphometric contours (m) and station locations in the northwest bay region of Eau Galle Reservoir. Shaded area represents regions of macrophyte growth (littoral zone)

Chambers were filled with distilled water purged with nitrogen to remove dissolved oxygen (DO). Nucleopore dialysis membranes (1.0-μm pore size) were secured onto the water-filled chambers with an acrylic plate. Immediately thereafter, the peepers were placed in a nitrogen-purged distilled water bath to maintain anoxic conditions during peeper deployment. The peepers were driven 6 cm into the sediment, which allowed exposure of four chambers to the interstitial water of the littoral-sediments and two chambers to the water column immediately above the littoral sediment interface. Peepers were equilibrated for 14 days (Shaw and Prepas 1989) before collection.

Upon retrieval of the peepers, water samples from each chamber were collected with acid-washed 50-ml syringes, then filtered immediately through a 0.45-μm membrane filter and sealed in a small acid-washed vial with minimal exposure to air. The samples were analyzed for SRP within 2 hr of retrieval.

Fickean diffusional fluxes (J) of P across the littoral-sediment interface were calculated (from Berner 1980), as

$$J = -\Phi \cdot D \cdot \Theta^{-2} \cdot dC/dx$$

where

Φ = porosity (0.8) of the sediment
D = areal sediment diffusion coefficient (1.24×10^{-9}) (Quigley and Robbins 1986)
Θ^{-2} = tortuosity of sediment ($\Phi^{-0.8}$) (Berner 1980)
dC/dx = P gradient across the littoral-sediment interface

Phosphorus gradients across the littoral-sediment interface were calculated from P concentrations immediately above and below (2-cm interval) the littoral-sediment interface.

Limnological Profiling

Six stations were established along a transect located in the northwest bay region of the reservoir (Figure 1) for monitoring seasonal changes in limnological conditions pertinent to the investigation. Stations 1 and 2 (0.65 m deep) were located within the macrophyte-occupied littoral zone; stations 3 and 4 (1.0 and 2.0 m deep, respectively) were located near the littoral-pelagic interface; and stations 5 and 6 (4.0 and 7.0 m deep, respectively) were located within the pelagic zone. Vertical profiles of pH, DO, total P (TP), and SRP were obtained at these stations over biweekly intervals from June through early September 1989. All data reported here derive from samples taken and measurements made between 2000 and 2200 hr, a period occurring typically at the onset of nighttime water column cooling during the summer in Eau Galle Reservoir.

Dissolved oxygen and pH were measured with a Hydrolab Surveyor II, which was precalibrated with buffers and Winkler DO determinations (American Public Health Association 1985). In situ profiles of pH and DO were determined at 25-cm depth intervals at stations 1-3 and at 50-cm depth intervals at stations 4-6 from the reservoir surface to within 15 cm of the sediment surface.

Samples for both TP and SRP analyses were collected with pneumatically driven close-interval syringe samplers, as described in James and Barko (1991). Filtration for SRP was accomplished in situ by attaching 0.45-μm membrane syringe filters to syringes. At the littoral zone stations (1-3), samples were collected over 5-cm intervals between 5 and 20 cm above the sediment, and at 12- to 25-cm intervals thereafter to the reservoir surface. At the pelagic zone stations (4-6), samples were collected over 25-cm intervals from 5 cm above the sediment to the reservoir surf.ce. TP was analyzed on a Technicon Auto-Analyzer II following digestion with potassium persulfate (American Public Health Association 1985). SRP was analyzed colorimetrically on a Perkin-Elmer Lambda 3b spectrophotometer using the ascorbic acid method (American Public Health Association 1985). The detection limit for all TP and SRP analyses was 0.005 mg L^{-1}.

Exchanges Between Zones During Nighttime Cooling

Water temperature was measured every 30 min at stations 1, 2, 5, and 6 (Figure 1) from May through September 1989 using recording thermistor strings (OmniData International) calibrated to the nearest 0.1 °C. These measurements were made from the surface downward at 0.25-m depth intervals at stations 1 and 2, at 0.5-m depth intervals at station 5, and at 1.0-m depth intervals at station 6. Wind speed (representing an average of 5-min intervals over 30 min) and air temperature (OmniData International) were recorded at station 3 every 30 min.

Water temperatures were integrated vertically over the entire water column of the littoral zone (stations 1-2) and over the upper 1-m water column of the pelagic zone (stations 5-6) to examine the development of horizontal gradients in water temperature between the littoral and pelagic zones during nighttime convective cooling. Horizontal water temperature gradients were calculated as the difference between depth-integrated water temperatures in the littoral and pelagic zones for each 0.5-hr interval. Mean negative horizontal temperature gradients were calculated for periods in which depth-integrated water temperatures in the littoral zone were cooler than those in the pelagic zone.

Hydraulic exchange rates during nighttime cooling were determined from patterns of dye dispersion between the littoral and pelagic zones. A transect was established in the vegetated region of the northwest bay, along the slope of the basin, using posts driven into the sediment at 10-m intervals (Figure 1). Buoys were placed in the pelagic zone at 10- to 20-m intervals to extend the transect into the open water. All stations and distances along the transect were surveyed using a transit.

Hydraulic exchange rates were determined at fixed biweekly intervals under prevailing climatic conditions from June through August 1989 using Rhodamine WT red fluorescent dye (Crompton and Knowles, Inc.) as a tracer. Methods for determining hydraulic exchange rates from dye dispersion were similar to those described in James and Barko (1991). The dye was injected homogeneously in the littoral water column (1.0 m deep) near the outer edge of the macrophyte beds interface (Figure 1) at 2100 hr during each monitoring period. Both the forward (into the pelagic zone) and reverse (into the littoral zone/macrophyte beds) edges of the dye cloud were tracked between 0600 and 1200 hr the next morning with a Turner Designs fluorometer (10-005R), calibrated with dye standards. Hourly volumetric flow rates (m^3 hr^{-1}) into the littoral and pelagic zones were calculated as the product of flow velocity (distance of the edges at $time_2$ minus the distance at $time_1$ divided by $time_2$-$time_1$), vertical expanse of the dye cloud edges, and horizontal length of the littoral-pelagic interface (about 1,000 m) divided by time (James and Barko 1991).

TP exchange rates (mg m^{-2} hr^{-1}) into the littoral or pelagic zone were calculated as the product of hourly volumetric flow rates and depth-integrated TP in the region of flow divided by the reservoir surface area. TP from the bottom 0.25 m of the littoral zone was assumed to move with dye into the pelagic zone, while TP from the top 0.75 m of the pelagic zone was assumed to move with dye into the littoral zone. These assumptions are based on patterns of dye dispersion observed earlier in this reservoir (James and Barko 1991), as well as in the current investigation. Net TP flux rates (mg m^{-2} hr^{-1}) were calculated as the difference between TP exchange rates into littoral and pelagic zones.

3 Results

Littoral-Pelagic P Gradients

Rates of SRP release from littoral sediments, measured in the laboratory at 20 °C, increased with increasing pH under both aerobic and anaerobic conditions (Figure 2). Under anaerobic conditions at lower values of pH, sediments exhibited higher rates of SRP release than under aerobic conditions. However, near pH 10, sediments exhibited similar rates of SRP release under aerobic and anaerobic conditions.

Ranges in rates of SRP release from littoral sediments in the reservoir were estimated during the period June through August using the linear relationships established between pH and rates of SRP release from littoral sediments measured in the laboratory (Figure 2). Predominantly aerobic conditions (DO > 1.0 mg L^{-1}) prevailed during the evening hours throughout the summer in the littoral zone; however, anoxia may have developed directly at the sediment surface, particularly during the late night and morning hours. Mean daily temperatures above the littoral sediments were 20 °C or greater (mean = 21.5 ± 0.03 standard error, SE) on 85 percent of the days measured during this period. Mean pH in bottom waters of the littoral zone ranged from >9.0 (range = 9.1 to 9.4) in June and July to 8.8 in August. Estimated rates of SRP release from littoral sediments ranged from 1.9 to 5.0 mg m^{-2} day^{-1} (mean = 3.6 mg m^{-2} day^{-1} ± 0.5 SE) under aerobic conditions and from 5.5 to 7.6 mg m^{-2} day^{-1} (mean = 6.7 mg m^{-2} day^{-1} ± 0.3 SE) under anaerobic conditions.

SRP in the interstitial water of littoral sediments increased significantly at most depths below the sediment interface between late May and August (Figure 3). Significant differences in SRP in the interstitial water as a function of sediment depth were not observed, however, due to high variability among replicates (analysis of variance, SAS 1985). SRP gradients across the littoral-sediment interface ranged between 3.4 and 7.3 × 10^4 mg m^{-4} (mean = 5.0 × 10^4 mg m^{-4} ±5,100 SE), resulting in a mean diffusional flux of 3.6 mg m^{-2} day^{-1} (±0.4 SE) for midsummer. This value was in agreement with the mean rate of SRP release from littoral sediments estimated for aerobic conditions under high ambient pH.

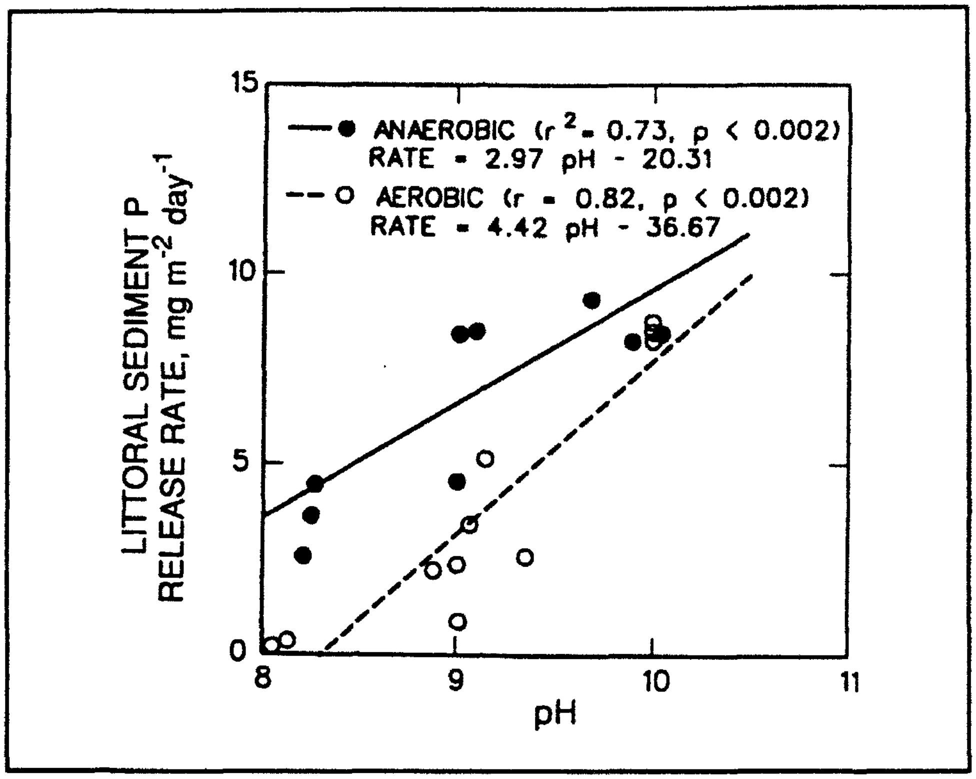

Figure 2. Variations in rates of SRP release from littoral sediments as a function of pH under aerobic and anaerobic conditions for undisturbed laboratory sediment incubation systems

Marked horizontal and vertical gradients in TP developed in the littoral zone from May through August (Figure 4), and SRP accounted for 45 to 90 percent of the measured TP. TP was generally much lower in the epilimnion of the pelagic zone than in the littoral zone. Elevated TP at metalimnetic depths (2 to 4 m) in the pelagic zone in early July and early September coincided with intrusion of storm inflows from the Eau Galle River (James and Barko, unpublished data). TP also increased in the hypolimnion of the pelagic zone from June through August. TP gradients both in the littoral and pelagic zones diminished in September as water temperatures decreased and the macrophyte beds entered senescence.

Thermal Gradients and Convective Circulation

Mean negative horizontal temperature gradients (littoral zone water temperature < pelagic zone water temperature) generally increased during declines in mean daily air temperature (Figure 5). However, this relationship was not statistically significant. Mean negative horizontal temperature gradients developed on 72 percent of the midsummer days (June-August, Figure 5) and averaged 0.41 °C (±0.04 SE). During seasonal warming in late May and June, mean negative horizontal temperature gradients developed only during

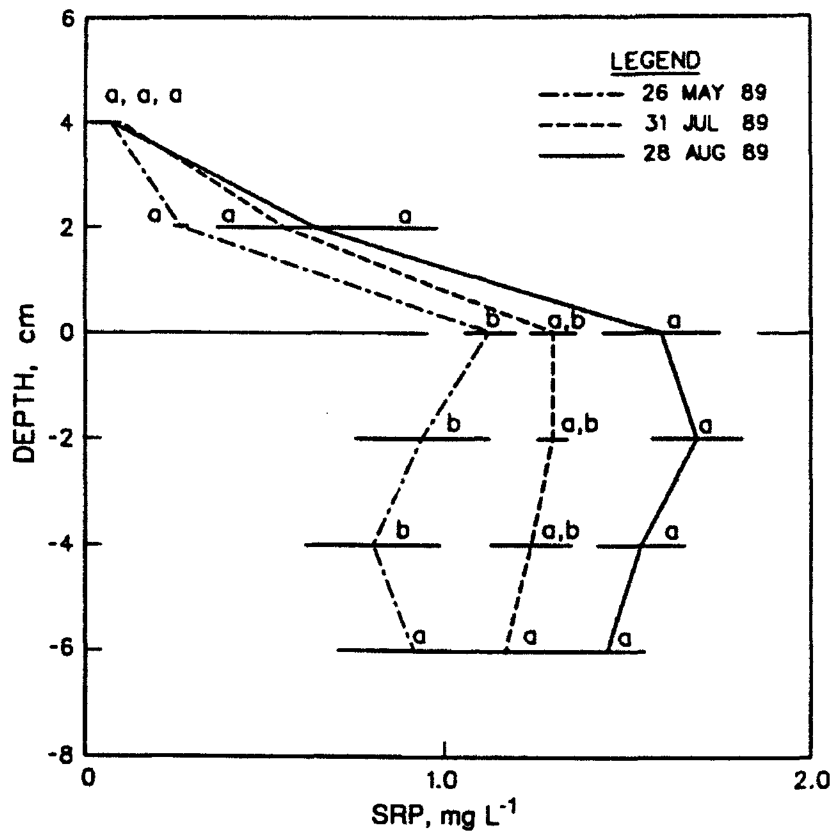

Figure 3. Seasonal variations in mean (± 1 SE; $n = 3$) SRP concentrations in the interstitial water of littoral sediments and overlying water column measured at station 2. Different letters indicate significant differences ($p < 0.05$) between dates, based on Duncan's multiple range analysis (SAS 1985)

periods when cold fronts passed through the region. Thus, only 31 percent of the days monitored in May and 43 percent of those monitored in June exhibited mean negative horizontal temperature gradients. In July and August, however, mean negative horizontal temperature gradients developed on 81 and 95 percent of the days, respectively.

During each dye-tracking investigation, the littoral zone exhibited cooler depth-integrated water temperatures than the pelagic epilimnion during the night and morning hours (Figure 6). Mean negative horizontal temperature gradients during these hours were greatest in early July and early August (Table 1). During midday hours of each investigation, the opposite pattern usually occurred, with depth-integrated water temperatures in the littoral zone exceeding those in the pelagic zone (Figure 6). Wind speed was generally greatest during the day, and declined to <2 m sec^{-1} at night during each

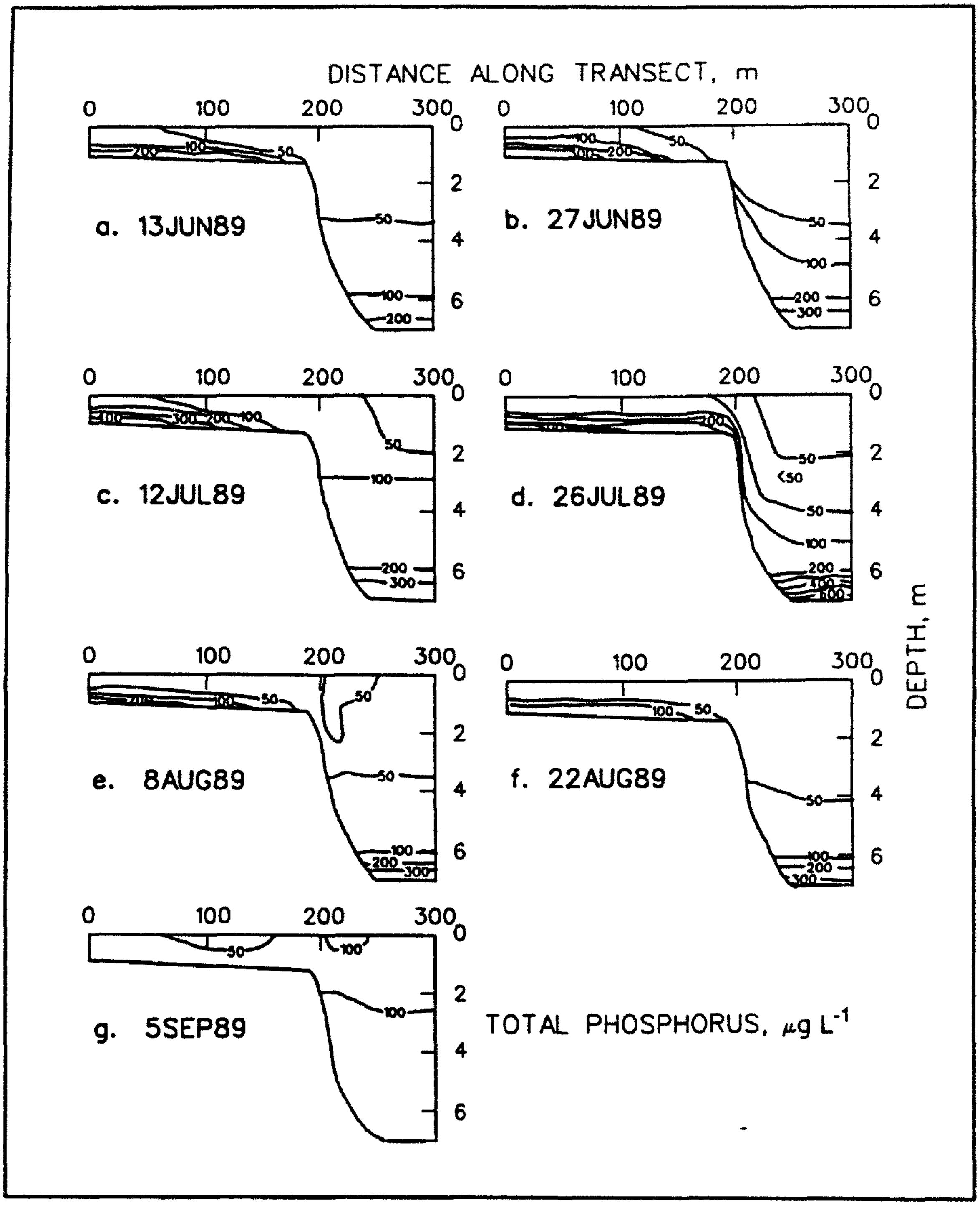

Figure 4. Seasonal, vertical, and horizontal variations in TP concentration in the littoral and pelagic zones

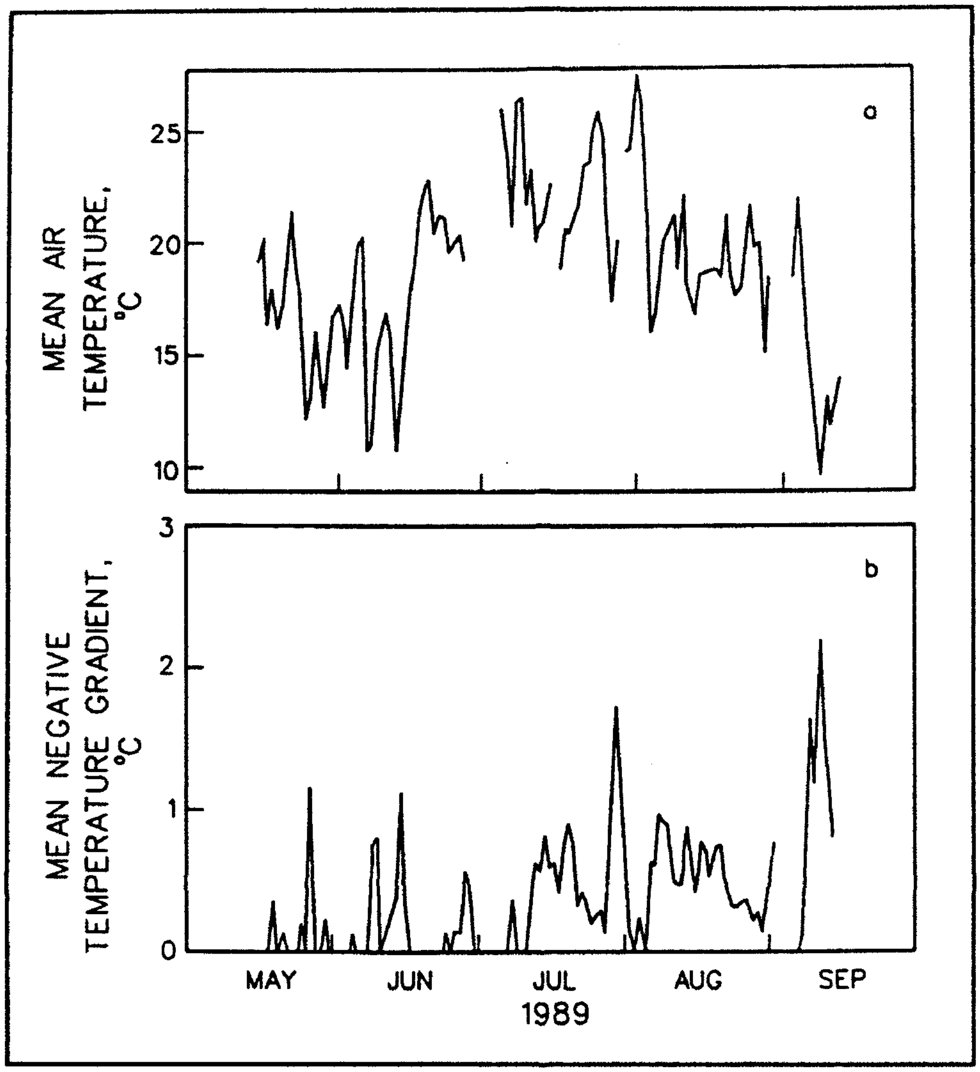

Figure 5. Seasonal variations in mean daily air temperature (a) and mean negative horizontal temperature gradients (b)

investigation. Wind speed was near zero at night in late June, late July, and early August (Figure 6).

Dye dispersed as a bottom current from the littoral zone to the pelagic zone at night (Figure 7). Intrusion of littoral water into the pelagic zone occurred as an interflow, consistently confined to 0.25 m in vertical expanse. The temperature of this interflow coincided with temperatures measured in the littoral zone (Figure 7). Due to seasonal variations in pelagic thermal stratification, the depth of interflow decreased to a minimum in July, then increased in August.

Hourly volumetric flow rates into both the littoral and pelagic zones were similar throughout the study, indicating an approximate balance in water exchange between the two zones (Table 1). Hourly volumetric flow rates

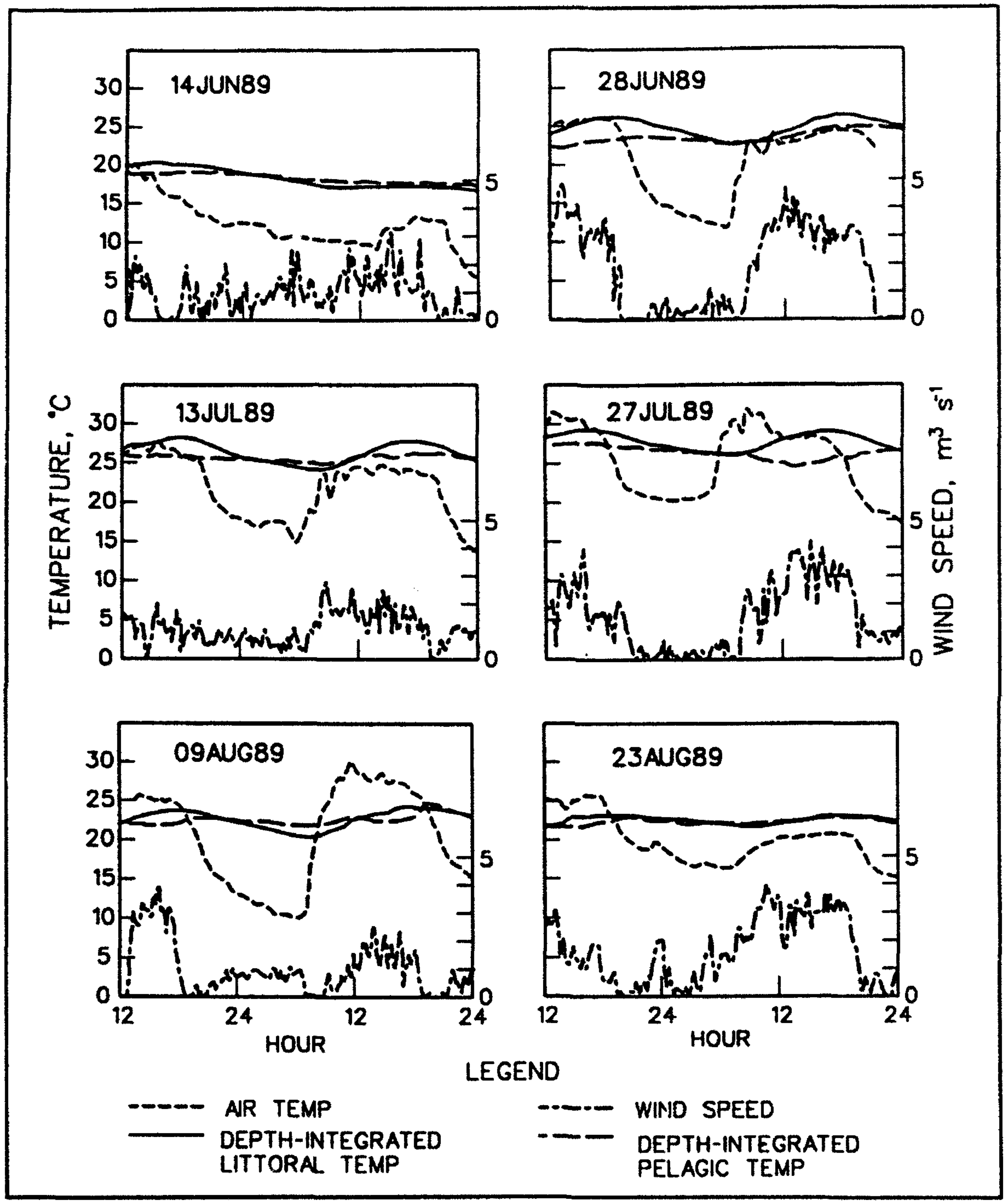

Figure 6. Diel variations in air temperature, depth-integrated littoral and pelagic water temperature, and wind speed (near the bottom of each panel) on 14 June, 28 June, 13 July, 27 July, 9 August, and 23 August 1989

Table 1
Estimation of Hourly Volumetric Flow Rates (Calculated from Dye Movement Patterns) and Mean Negative Horizontal Temperature Gradients During Periods of Nighttime Convective Circulation

Date	Direction of Movement	Flow Velocity m sec^{-1}	Volumetric Flow Rate m^3 hr^{-1} $\times 10^3$	Mean Volumetric Flow Rate m^3 hr^{-1}	Mean (± 1 SE) Horizontal Temperature Gradient[1] °C
13-14 Jun 89	Pelagic Littoral	0.0017 0.0005	1.5 1.4	1.4	-0.41[b] (0.06)
27-28 Jun 89	Pelagic Littoral	0.0012 0.0004	1.1 1.1	1.1	-0.16[c] (0.02)
12-13 Jul 89	Pelagic Littoral	0.0036 0.0012	3.2 3.1	3.2	-0.58[b] (0.07)
26-27 Jul 89	Pelagic Littoral	0.0010 0.0003	0.9 0.8	0.9	-0.13[c] (0.01)
8-9 Aug 89	Pelagic Littoral	0.0051 0.0017	4.6 4.7	4.6	-0.94[a] (0.08)
22-23 Aug 89	Pelagic Littoral	0.0022 0.0009	2.0 2.3	2.1	-0.22[c] (0.03)

[1] Different letters indicate significant differences at the 5-percent level of probability or less (Duncan's multiple range analysis, SAS 1985).

were greatest in early July and early August, coinciding with the occurrence of relatively large mean negative horizontal temperature gradients (Table 1). The lowest hourly volumetric flow rates were observed in late June and late July, coinciding with minimal mean negative horizontal temperature gradients. A strong linear relationship existed between hourly volumetric flow rates and mean negative temperature gradients (flow = 4.38 • mean negative horizontal temperature gradient + 0.44; $r^2 = 0.86$; $p < 0.005$) (SAS 1985), suggesting that differences in water temperature between littoral and pelagic zones accounted for most of the variation in hourly volumetric flow rates.

P Exchange Dynamics

Hourly TP exchange rates to both the littoral and pelagic zones were greatest in early July and early August and lowest in June (Table 2). TP exchange rates to both zones were a function of both the volumetric flow rate and TP in the region of flow. Estimated hourly TP exchange rates to the pelagic zone were greater than to the littoral zone, as the result of higher TP in the littoral bottom waters (Table 2). Mean summer TP in the region of flow in the littoral zone (118.0 mg m^{-3}; ±15.7 SE) was over 2 times greater than in the region of flow in the pelagic zone (44.5 mg m^{-3}; ±2.8 SE). Net TP flux to the pelagic zone, at rates ranging between 0.12 and 0.43 mg m^{-2} hr^{-1}, occurred

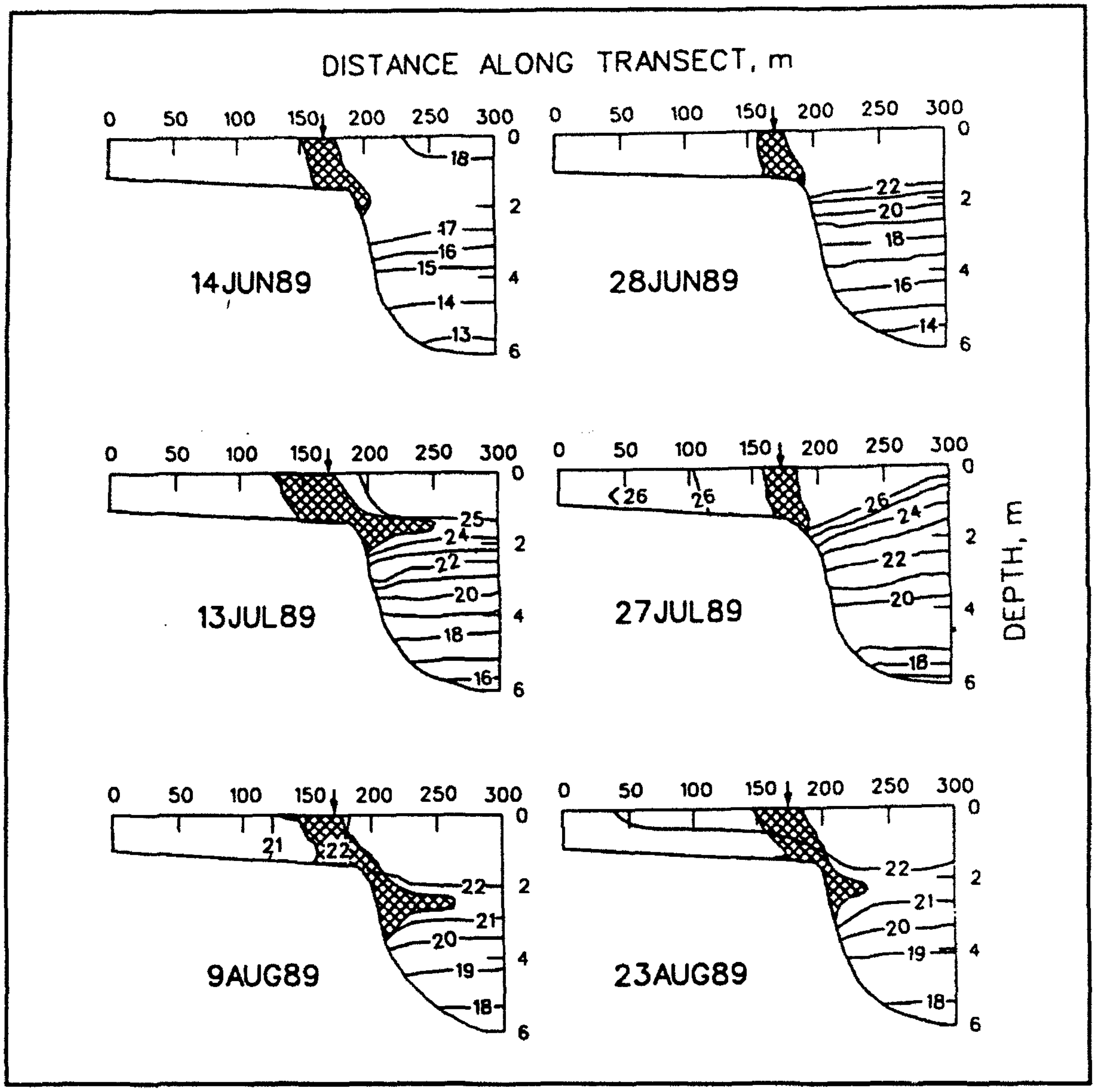

Figure 7. Vertical and longitudinal variations in water temperature (°C) measured at 0600 hr, and the position of the dye cloud measured between 0600 and 1200 hr on 14 June, 28 June, 13 July, 27 July, 9 August, and 23 August 1989. Shaded areas represent position of dye cloud

during all dye-tracking investigations (Table 2). Using an overall mean volumetric hydraulic flow rate of 1,770 m^3 hr^{-1} (determined from the relationship between hourly volumetric flow rates and a mean negative horizontal temperature gradient of 0.41 °C) and mean TP in the region of flow, a mean net TP flux of 0.22 mg m^{-2} hr^{-1} to the pelagic zone was calculated for the midsummer period.

Table 2
Estimation of Hourly TP Exchange Rates Between Littoral and Pelagic Zones, and Net TP Flux to Pelagic Zone During Dye-Tracking Periods

Date	Direction of Movement	TP $mg\ m^{-3}$	Hourly TP Exchange Rate $mg\ m^{-2}\ hr^{-1}$	Net TP Flux to Pelagic Zone[1] $mg\ m^{-2}\ hr^{-1}$
13-14 Jun 89	Pelagic Littoral	91.5 40.3	0.22 0.10	0.12
27-28 Jun 89	Pelagic Littoral	124.8 35.8	0.22 0.06	0.18
12-13 Jul 89	Pelagic Littoral	134.6 52.8	0.71 0.28	0.43
26-27 Jul 89	Pelagic Littoral	184.3 43.8	0.27 0.06	0.21
8-9 Aug 89	Pelagic Littoral	87.0 52.2	0.67 0.40	0.27
22-23 Aug 89	Pelagic Littoral	85.6 42.0	0.30 0.15	0.15

[1] Difference between hourly TP exchange to the littoral and pelagic zones divided by the reservoir surface area (0.6 km^2).

4 Discussion

Rates of P release from littoral sediments in macrophyte beds of Eau Galle Reservoir, measured in the laboratory, were linearly related to pH under both aerobic and anaerobic conditions. As in our investigation, other studies have shown that pH can have a regulating effect on rates of P release from sediments, particularly under aerobic conditions (Lee, Sonzogni, and Spear 1977; Drake and Heaney 1987). Enhanced ligand exchange on iron hydroxide particles at high pH is thought to be an important mechanism in elevated rates of P release from sediments under aerobic conditions (Drake and Heaney 1987). At lower pH values, however, P release from littoral sediments appears to be minimal under aerobic conditions. This pattern may be attributed to the potentially more important effects of an anaerobic environment on P release at lower pH. Estimated rates of P release from littoral sediments at high pH under aerobic conditions were in agreement with diffusional fluxes estimated independently from sediment peepers, representing 44 percent of the mean reservoir-wide internal P loading rate of 8 mg m^{-2} day^{-1}, measured for the summer by mass balance in Eau Galle Reservoir (James, Barko, and Taylor 1991).

TP gradients in the littoral macrophyte beds were prominent throughout much of the summer, and SRP accounted for a large percentage of littoral TP. To our knowledge, no investigations have shown such marked concentration gradients vertically in the littoral zone or horizontally between littoral and pelagic zones. These observations, in combination with results obtained in our laboratory incubation systems and sediment peepers, strongly suggest that littoral sediments in macrophyte beds provide an important source of P to the reservoir. Lower P concentrations in the surface waters of the littoral zone may be the result of P uptake from the water by *Ceratophyllum demersum*, since the foliage of this species is most dense near the water surface (James and Barko, personal observation). In addition, strong thermal stratification in the littoral zone during the day (James and Barko 1991, unpublished data) may restrict upward movement of sediment-derived P to surface waters via mixing.

Nighttime convective circulation constituted an important mechanism for movement of littoral P to the pelagic zone during the summer. During the night and morning, cooler bottom water from the littoral zone moved as an interflow current into the pelagic zone at the base of the epilimnion, and was replaced by a return current of warmer surface water from the pelagic zone. The hourly volumetric flow rate was strongly related to the mean negative horizontal temperature gradient between the littoral and pelagic zone, indicating that convective cooling was responsible for this hydraulic exchange pattern. Reasons for seasonal variations in the mean negative horizontal temperature gradient are complex, but appear to be related to the rate of air temperature cooling, wind effects, relative humidity, and the equilibrium temperature (Stefan, Horsch, and Barko 1989). The frequency of occurrence of negative horizontal temperature gradients, and therefore nighttime convective circulation, was lowest in June, but increased substantially in July and August. These seasonal variations are of clear importance when considering the magnitude of littoral P flux as affected by nighttime convective circulation.

We have focused exclusively on nighttime convective circulation as a mechanism transporting littoral P in an underflow to the pelagic zone of Eau Galle Reservoir. However, Monismith, Imberger, and Morison (1990) have shown recently for another small reservoir that a convective overflow pattern can occur during daytime heating as warmer littoral water moves as a surface flow into the pelagic zone. Based on our analysis of thermal data, these daytime overflow patterns may occur in Eau Galle Reservoir as well (James and Barko, unpublished data). However, since surface concentrations of P in the littoral zone were typically low, and often similar to those measured in the pelagic epilimnion (Figure 4), we maintain that net TP flux to the pelagic zone of Eau Galle Reservoir during the day is probably minimal.

During the current investigation, it was assumed that hydraulic and P exchanges determined at a single location in Eau Galle Reservoir were representative of the entire littoral zone. However, variations in the slope of the littoral zone may influence the rate of water cooling, because of differences in volume between littoral and pelagic zones. Differences in slope may also affect the rate of bottom water movement from the littoral zone, as a result of differences in gravitational acceleration. The effects of differing macrophyte densities, both vertically and horizontally in the water column, on hydraulic exchange rates also need to be considered.

Prentki et al. (1979) estimated a net P flux rate of 3.2 mg m^{-2} day^{-1} for Lake Wingra, due to wind-induced circulation. However, since the northwest bay (region of study) of Eau Galle Reservoir is well protected from northern and western winds by surrounding hills, and is densely populated by *C. demersum* (Filbin and Barko 1985; James and Barko, personal observation), the effects of wind on the circulation patterns examined in this reservoir are considered to be relatively minor. Obviously, this may not apply to other systems (e.g., Lake Wingra) with greater fetch, surface area, or exposure to winds.

Although nighttime convective circulation has been identified as an important transport mechanism for littoral P in Eau Galle Reservoir, it is not possible to calculate precisely the daily net TP fluxes, since we have no accurate measure of the period over which nighttime convective circulation occurred.

In earlier investigations, the linear movement of dye in this reservoir was used as a measure of nighttime convective circulation time (James and Barko 1991); however, this information was not obtained in the present study. It is possible, however, to roughly determine the period of nighttime convective circulation as the time during which negative horizontal temperature gradients occurred. This period averaged 9.6 hr ($\pm$0.9 SE) during midsummer, resulting in an estimated mean daily net TP flux of 2.1 mg m^{-2} day^{-1} to the pelagic zone. This flux rate represents about 60 percent of the estimated rate of P release from littoral sediments under aerobic conditions (3.6 mg m^{-2} day^{-1}) and 26 percent of the reservoir-wide internal TP loading rate for the summer (James, Barko, and Taylor 1991).

5 Conclusions and Recommendations

On a daily basis, the water in macrophyte beds of shallow littoral zones heats and cools more rapidly than adjacent open water, partly as the result of differences in mixed volume, but also because of the presence of vegetation. Submersed aquatic macrophytes contribute significantly to the development of thermal gradients, which promote convective hydraulic circulation. Effects of convective hydraulic circulation are potentially far-reaching, since this mechanism operates daily and can account for massive transport of dissolved constituents between littoral and open-water regions of lakes and reservoirs. In Eau Galle Reservoir, as reported here, convective transport from aquatic macrophyte beds in the littoral zone accounted for about 26 percent of the internal load of phosphorus to the reservoir.

For other aquatic systems, detailed diel observations of both water temperature and periods of flow will be necessary to estimate convective circulation time, which is critical to the accurate estimation of daily horizontal TP fluxes. Investigations of hydraulic and P exchanges during convective circulation need to be conducted under a variety of morphometric and climatic conditions to evaluate for other aquatic systems the significance of littoral P transport shown to be important in Eau Galle Reservoir. In addition, it is important to evaluate the effects of different types and amounts of submersed aquatic macrophytes on convective circulation. This latter point is particularly relevant, since unlike the littoral zone of Eau Galle Reservoir (dominated by the non-rooted *Ceratophyllum*), most littoral zones are dominated by rooted aquatic macrophytes.

Information on rates and volumes of water exchanged in littoral macrophyte beds as a result of convection and other processes will be useful in estimating transport and dilution rates for a variety of solutes, including herbicides. For herbicides specifically, decisions on herbicide type, formulation, concentration, and time/season of application will be directly benefited. This information will also be useful in assessing the influences of aquatic macrophytes on eutrophication.

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13. ABSTRACT *(Maximum 200 words)*

Phosphorus (P) dynamics in aquatic macrophyte beds and P exchanges between littoral and pelagic zones, driven by nighttime convective circulation, were examined in Eau Galle Reservoir, Wisconsin, during summer 1989. Rates of P release from littoral sediments, measured in laboratory incubation systems, increased in a linear fashion with pH under both aerobic and anaerobic conditions. Estimated rates of P release from littoral zone sediments, based on field measurements of pH and oxygen, averaged 3.6 mg m^{-2} day^{-1} under aerobic conditions, and were in close agreement with independently determined diffusional fluxes across the littoral sediment interface. Marked vertical gradients in P developed during the summer in bottom waters of the littoral zone. The littoral zone, dominated by submersed macrophytes, cooled more rapidly at night than the pelagic zone on 72 percent of midsummer days (June-August), promoting nighttime convective circulation. Based on patterns of dye dispersion during these periods of circulation, cooler littoral bottom water originating within macrophyte beds moved into the pelagic zone as an interflow confined to the base of the epilimnion, while warmer pelagic water moved into the littoral zone as a surface flow. Hourly volumetric flow rates were linearly related to mean negative horizontal

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temperature gradients that developed during the night. Net TP flux from the littoral to the pelagic zone ranged from 0.12 to 0.43 mg m^{-2} hr^{-1} and averaged 0.22 mg m^{-2} hr^{-1} for the summer. Nighttime convective circulation appears to be an important mechanism for movement of littoral P from macrophyte beds to the pelagic zone in this reservoir.

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Limnology	Solutes
Littoral zone	Temperature
Macrophytes	